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THE ORIGIN OF SPECIES BY MUTATION.

HISTORICAL REVIEW.

a. THE CONCEPTION OF THE SPECIES AND PRE-DARWINIAN EVOLUTION

PRIOR to the publication of the work of Darwin, and contemporaneous with him, there obtained several widely differing opinions concerning the origin of species. There was the philosophical school, in which the most prominent figures were Lamarck and Geoffrey St. Hilaire, defending the common origin of all species. There were those who regarded the genera as created and the species and subspecies as derived from these. There were the adherents of the Linnæan species who insisted that these were created. Finally there were others who regarded the elementary forms which proved constant under cultivation as created.

The theories of the times were dependent upon the extent of exploitation of the systematic opportunity. Before Linnæus the genera were commonly accepted as the systematic units, and the species regarded as their minor modifications. Numerous genera had common names, while the species were usually not so distinguished. The view that the genera were created and that the species had originated from them by transmutation had many advocates. Many things show that the present conception of a species was hardly known before the time of Linnæus. In the older works on natural history, a very short diagnostic description was written after the generic name, and as often as the plant was mentioned this diagnosis was, of necessity, repeated. So long as the number of plants

recognized was small, this occasioned no great inconvenience, but with more detailed and extensive investigations the originally brief diagnosis could not but become elaborate and detailed. The simplification of this complex and unwieldy mechanism was the work of Linnæus, who proposed the binary system of nomenclature, in which the plant or animal is described and assigned a specific name to replace the brief description previously appended to the generic name. To give the essential authority to his system, he made the species the units; and his predecessors and he himself in earlier years had regarded the genera as created and the species derived from them, he now maintained that the species had been created and that the minor forms had arisen from them in a natural manner.

But the Linnæan species are collective species. He himself seems to have recognized this fact more clearly than his followers, although he rarely distinguished varieties among his species and forbade his students their study, as has been said by some to assure so far as possible the dignity of his new systematic units. The history of the period following the establishment of this new system is similar in many respects to the earlier times when the genera were regarded as the units. While the unstudied material was copious and easily accessible, there was no reason to ignore the master's injunction against the study of minor forms or to doubt that they were descended in a natural manner from the created species. As the material, especially in the European flora, was more thoroughly studied and the opportunity for descriptive work became less, the necessity of considering minor forms became increasingly greater, until it was clearly recognized that the Linnæan species are built up of a number of forms showing small but clearly defined differences. Probably the finest illustration is *Draba verna,* a species described by Linnæus himself, which has been split up into over two hundred minor species. *Viola tricolor* has suffered a very similar fate. Not only were these minor species found to be distinguished by small but sharply limited morphological characteristics, showing well defined differences, not of one but often of all the parts, so that a comprehensive characterization is of necessity

very extensive, but they also proved themselves quite true to seed under cultivation. Many of them, grown for many generations, proved quite as true to their minute differences as did the larger groups currently dignified by the term species. Individual variability was everywhere seen by the students of these minor forms, but the transition from one form to another, never, and it was but natural that they should regard species as immutable. They opposed the transmutationists and adherents of the Linnæan school, basing their contention upon the Biblical records and the constancy of the minor species through a series of generations, and dismissing as artificial and arbitrary the grouping of such real forms into larger "species."

The contest before Darwin led to two important results, the experimental demonstration of the existence of numerous constant, independent types of the Linnæan species, and the very general conviction that such constant types had arisen by transmutation, as the process was generally designated at that time, from the larger units. There were four more or less clearly distinct conceptions of the origin of species. The adherents of these schools were prepared in very different degrees for the revolutionary writings of Darwin. Those least prepared for the new doctrine were the adherents of the minor species. Variation they knew very well, but this never led to the transgression of specific bounds, and mutation they never saw. And yet it is strange that this escaped these keen observers, for it is to be oserved both in cultivation, where it produces the so-called single variations, and in nature as well.

b. THE THEORIES OF DARWIN AND WALLACE AND THE HYPOTHESIS OF MUTATION.

To have generally established the theory of descent, the scientific explanation of systematic relationship, is the immortal honor of Darwin. In doing this he revolutionized biological science and influenced most profoundly all other fields of intellectual activity. At and before the time of the publication of the *Origin of Species* the origin of varieties from the species was generally admitted. He insisted that "varieties are incipient species" and that "species

have descended, like varieties, from other species." For the establishment of these fundamental hypotheses he collected data still of great value in present work in the same field. The task of Darwin was the establishment of the theory of descent, and his work was so effectively done that this is now generally accepted. The theory of descent finds its support in the data of comparative morphology, embryology, and paleontology. This is very different from that upon which the physiological side of the theory of evolution must be based, and upon just this side of the question the great master was never quite clear, or at least never expressed himself finally. In his earlier works it was the spontaneous variations to which he attached the greatest importance as material for natural selection, while in his later works, and under the influence of his critics, he attributed more significance to individual variability, though between the two he never sharply distinguished. Such was not necessary to his main task and would have introduced many difficult problems whose solution, had data for their elucidation been available, was not necessary for the establishment of the great theory and would only have detracted from the main object. Quotations might be cited to show Darwin's attitude toward the two kinds of variability, which he surely recognized, but between which he never very closely distinguished; but so long as it is borne in mind that he did recognize and distinguish *individual differences* and *single variations,* and that he did ascribe to the latter a very significant rôle in the origin of species, it is hardly necessary to discuss in detail the different ways in which he has expressed his valuation of the two types of variability as material for natural selection.

In his attitude toward this question—fundamental for future evolutionary work though not for the establishment upon comparative grounds of the broad lines of his theory—he showed all his characteristic caution, even exhibiting some of the weak points of his theory to those who were glad enough to avail themselves of any assistance in the criticisms they were so eager to hurl against it. It was another who restated the theory of Darwin, and in a simpler, more attractive form. Wallace presented to the public a work

on Darwinism in which he attempted to show that species are the product of the selection of the differences of individual variability. His great purpose was to show that animals and plants do perpetually vary in the manner and to the amount requisite for the formation of new specific forms." The single variations of Darwin he regarded as quite without significance in descent. Not only did he assume as the basis of his theory a rapid increase in numbers with the consequent early death of numberless individuals, variability, and the survival of the fittest in the struggle for existence, but he went even further and assumed as an additional principle the inheritance of variations and the bettering of the race through the selection of the breeder. But the meaning of the term "race" must be very carefully defined. The various cultivated plants whose specific identity with wild forms is hardly to be recognized, are by no means necessarily the result of selection of individual variations. Many of the cultivated races are as old or older than their cultures; they are minor species, and their origin from a given wild form is as much a matter of conjecture as that of the common ancestry of the species of a genus. It must be said that it is upon very questionable grounds that Wallace concluded that: "It is therefore proved that if any particular kind of variation is preserved and bred from, the variation itself goes on increasing in amount to an enormous extent; and the bearing of this on the question of the origin of species is most important." This can only be assumed as a working hypothesis, not accepted as an established basis for further constructive work. That selection may carry individual variation to "an enormous extent," practically may be freely admitted, but this is very different from an enormous biological difference, and that it may extend to the "amount requisite" for the origin of specific form is a quite unestablished assumption. He shows the admirable explanation of the systematic and biological facts which the simplified theory of selection offers, but how the elementary or sub-species of which he furnished so many examples, originated, he does not satisfactorily prove. He does not show that the races produced by selection are constant when this selection is discontinued,

or that specific characters may actually be the product of the action of selection upon the material of individual variability.

It must not be thought by those not well acquainted with the literature of evolution that the only critics of Darwin's theory have been those who opposed it on dogmatic grounds. The sufficiency of common variability with natural selection has often been called in question, and a paper upon the theory which has reached its present culmination in the two volumes of Professor DeVries would be incomplete without a brief mention of the attitude of some of those who have not joined in the general acceptance of natural selection.

Among the earliest of these was Cope, who granted that natural selection accounts for the survival of the fittest, but could not admit that common variability accounts for the origin of the fit, and for this he assumed special causes which he summarized as *Bathmism.* Semper discarded the explanations of selection and ascribed to the environment an important rôle, returning to the so-called *monde ambiant* of the French school. Upon the basis of a large series of data Louis Dollo declared that evolution is discontinuous, irreversible, and limited, thus opposing directly the logical conclusions to be drawn from the grounds assumed by Wallace.

A most important criticism of the current theory of descent is Bateson's well known *Materials for the Study of Variation, Treated with Special Regard to Discontinuity in the Origin of Species.* He maintains that the theory of descent must explain not only the relationship of organisms but their discontinuity as well. Species as they exist to-day are sharply separated from each other, and this great objection to the theory of gradual or continuous individual variation is not removed or surmounted by a reference to the numerous transitional forms which are to be found. These have been shown in many cases to be themselves sharply defined and constant units which, except for the amount of their differences, are just as deserving of specific designation as are the larger groups of forms, and do not indicate a continuous origin. Another important argument brought forth by Bateson against the selection theory is that it does not account for the useless differences which often appear as specific characters. Bateson concludes that: "The

evidence of variation suggests in brief that the discontinuity of species results from the discontinuity of variation."

The geologist Scott opposed many statements of Bateson's work, referring to the continuous paleontological series in which progress, so far as we may judge from the historical fragments, seems to have been by almost imperceptible gradations. But it must be seriously questioned whether the continuity of paleontological remains is not that of a series of numbers and the differences in this series such as Bateson would designate as steps, rather than the difference of continuous variability. The term mutation has been used in geology more than in any other field of study, and many important considerations are taken up by Scott.

Korschinsky termed the mutation or spontaneous changes of earlier authors "heterogenesis," and brought together a large number of examples of garden forms, often distinguished so sharply from the parent type that, were their origin not known, they would be designated by the systematist as distinct species, which originated suddenly and without transition, and he concluded from the examination of his data that in horticulture all new forms, or more properly all new characteristics, originate by heterogenesis. According to him new varieties are not secured by selection or accumulation of individual variations does not occur. Selection is a conserving element, fixing varying characteristics of previous origin and preventing further variation, but is not able to produce new forms. In his writings, then, the cardinal principles of the selection theory and the mutation theory are stated and contrasted.

Other expressions of dissatisfaction with the current selection theory have been many and from men who could speak with authority, but they cannot be detailed here.

THE SEVERAL KINDS OF VARIATIONS.

The mutation theory is very little concerned with the origin of the larger groups or with the broad outlines of the theory of descent. These rest upon comparative and historical data, and, so far as the scientific world is concerned, have long been firmly established. But with the physiological aspects of the evolution theory

it is quite different, and to it, especially to its experimental side. the author of the mutation theory directs our attention.

In a work dealing primarily with variation and its inheritance, the first thing to be done is to examine the different meanings of the term and discern exactly what it comprehends in the several phenomena which it has been made to cover. An analysis shows that under the term variability four essentially different phenomena have been included. There is the systematic polymorphism and the polymorphism produced by hybridization, there are the differences of organs and individuals obeying the law of Quetelet, and finally there are the so-called spontaneous modifications or single variations. For a clear understanding of the position occupied by the mutation theory these groups must be examined in some detail.

As to systematic polymorphism, the Linnæan species are collective species, artificial groups composed of a greater or lesser number of forms as sharply and completely distinguished from each other as the best species, but usually designated by the names of varieties and subspecies; varieties when they differ in but a single characteristic, but generally subspecies when they differ in the totality of their characteristics, in their habit, as it may be called.

In practice all possible differences of opinion upon this point have been defended by systematists. Some have insisted that these are elementary species and have given them binary names, breaking up the Linnæan species into minor forms. This is being done very extensively at the present time. The botanist who sees the mass of current literature can hardly look through the accumulation of a fortnight without finding papers devoted to the segregation of some of the older species. In Europe *Rubus,* the raspberry and blackberry, and in America *Crataegus,* the hawthorn, furnish striking examples.

A few years ago not a score of hawthorns were described for North America, while at the present time the number is ten times as great and being constantly increased. The most recently published flora of the Southern States contains 6300 species as compared with 3400 of the preceding flora of the same region, which was, however, published some years before. Such work is criticized un-

sparingly by many who see in it only confusion and useless labor, and insist that the characteristics of these new species are only individual variations, perhaps dependent upon special life conditions, pointing with unfeigned satisfaction to the cases where separate "species" have been described from the same plant when grown under different conditions. But evidence of special interest and importance is that furnished by *Draba verna,* a species of Linnæas which, as mentioned above, has since been divided into over 200 minor forms. Jordan had the most of these under cultivation in his garden and was so thoroughly convinced of their constancy as to regard the minor forms as created and species as immutable, while others have satisfied themselves in the same way of the constancy of many of the minor forms,

Some emphasize the minuteness of the differences which separate these minor forms from each other, and regard their use as specific characters as unjustifiable. Those of the opposite opinion point to the fact that these forms differ from each other not in a single or a few characteristics but in all, so that a complete description must be very elaborate, and to their constancy in culture, the lack of transition between the individual types or between these types and the ideal species from which they are supposed to have sprung. The treatment of these forms by the descriptive botanist must be largely a matter of judgment on the part of the one concerned with the elaboration of the group in hand. So long as consistency is maintained, it matters little whether they are designated as varieties or all given binary names. Possibly the most convenient and simple solution of the problem would be the establishment of a ternary nomenclature in which, with all the minuteness of subdivision characteristic of modern systematic work, the old familiar generic and specific names under which the complexes have long been known might be retained. The specialist would then refer to a plant by its generic, specific, and minor species name, while the amateur or the morphologist or physiologist would simply refer to the larger group, the genus or the genus and Linnæan species. But with all the talk of species, subspecies, varieties, and nomenclature it must not be forgotten that the essential question is whether

forms are actually differentiable and constant in their characteristics.

Before and since the time of Darwin it has been assumed that varities are of common ancestry, but only in the rarest cases is there a historical record. Even in the garden varieties this holds true; the record of their origin is generally wanting or untrustworthy. This part of the field of variability must be largely comparative; its data are morphological, and only very rarely is it to be approached from the historical or experimental side.

The polymorphism produced by hybridization is due to the changed combinations of the heritable characteristics of the parents. For scientific investigations the simplest possible combinations should be selected. The investigator selects the least "variable" species. The plant breeder, on the other hand, prefers parents of which at least one is very "variable," so that the range of variation of the hybrid may be increased and the possibility of securing a new form thus heightened. To a discussion of these problems a second paper is to be devoted, and so we shall not consider it further here.

Variability in its restricted sense, or individual variability, comprehends the differences of individuals and organs which are amenable to the law of Quetelet, which was formulated since the time of Darwin, and which, with the labors of Galton, Weldon, Bateson, Davenport, Duncker, and others of recent years has given rise to an entirely new phase of biological investigation, the statistical study of variation and heredity, and the application of the results of these studies to the problems of organic evolution. The results of these investigations show that common, individual, or fluctuating, variations group themselves around a mean value, the frequency of occurrence of individuals or organs varying on either side of the mean, decreasing as the degree of their deviation from the mode increases. In fact, when a large series of observations are taken and the curve plotted, it is found to coincide with the curve of the probability of error.

We may take an illustration from Professor DeVries's own work, though others equally good may be found in the literature

in almost unlimited number. Seeds of the common red-spotted garden bean were found to vary in length from eight to sixteen millimetres. In the lot of 448 beans, the numbers with the different lengths were found to be as follows:

Length, millimetres, . .	8	9	10	11	12	13	14	15	16
Number	1	2	23	108	167	106	33	7	1

It will be seen that by erecting upon a base line in which the different seed lengths serve as abscissas, ordinates corresponding in length to the number of beans in that class, and connecting these ordinates, a very symmetrical curve closely corresponding to that secured by the expansion of a binomial will be secured.

Numerous illustrations of this kind might be given. The fruit length of *Oenothera,* the number of the ray flowers of the Compositæ, the height, and weight, and strength of pull, and keenness of vision of man, as well as his social traits, all follow the same law. The validity of this law for various characteristics of a very large series of organisms, both animal and vegetable, has been established by direct observation and measurement. This type of variability has been variously designated as fluctuating, gradual, continuous, reversible, limited, statistical, and universal. Of these terms, individual has been used most frequently in zoological and anthropological studies, while the best general term is fluctuating or flowing. In botany there is a distinction to be made between individual and partial variability, the former designating the difference between individuals, the latter the equally numerous differences between the organs of the same individual. Darwin repeatedly insisted that this form of variation "perpetually occurs," and Wallace laid even greater emphasis on this point. It might then be termed perpetual or uninterrupted.

Now the generally accepted theory of natural selection is that environmental conditions continually select only a certain class or classes of individuals, or, to state it more precisely, eliminate all not having the peculiar characteristics adapting them to their life conditions. So in the course of a longer or shorter period of time one or more good species would be developed, showing as the fundamental distinguishing mark the perfection and fixation of the

fortunate variation which determined its superiority over all the other individuals in the competition for existence. Of course such new species would be expected to vary somewhat.

Let us use again the illustration of the bean and consider for the sake of argument that the small seeds have in some way a great advantage over the larger ones under the conditions in which the plants grow. In the course of a few or many generations all but small-seeded individuals would disappear. These would vary in length from four to twelve millimeters, but the most of the individuals would have a mean value. The curve would be similar to the original one but with a mean representing an entirely different species. Had the larger seeds been selected, the same thing would have occurred, but the mode of the new species would have been large instead of small.

Supposing that both large and small seeds were especially adapted to certain life conditions, then two divergent species would have been developed. There would be a form with large and another with small seeds, each showing a considerable range of variation. Perhaps this variation might be so great as to cause the limits of the species to overlap, so that a continuous series of lengths from the shortest of the short seeds to the longest of the long seeds would result, and from the measurement of any individual seed it would be impossible to say to which species it belonged. Such transgressive variability, as it is called, very frequently occurs.

This illustration may make clearer the distinction between common or fluctuating variability, and mutation, to which we must presently turn, and at the same time depict a purely hypothetical case of evolution by selection according to the theories of Darwin, or more especially Wallace, for it must be borne in mind that Darwin attached much importance to the single variations.

The illustration is not an altogether satisfactory one, since species are not based upon a single characteristic. But it is a very convenient one for illustrating the supposed action of selection, and for our present purposes it is unnecessary to assume a more complicated situation. One of the strongest supports for the Darwinian theory has always been the evidence of garden selection with its

consequent improvement. Many cases are known in which artificial selection has produced just such results as those we have assumed for the seed lengths in the bean. But for the origin of specific characters it is not necessary merely that a modification may be effected by selection. It must become fixed, become independent of selection.

"The true danger reef of the Darwinian theory is the transition from artificial breeding selection to natural selection," says Paul Janet. Garden selection has not yet secured the fixation of the modifications of selection. Common variability may also be termed linear variation, occurring as it does toward plus or minus. It is also characterized by reversion to the type. It does not lose its plasticity: the long- and short-seeded races of beans, to use again our illustration, might be developed with great ease, but so soon as selection ceased, the variations would again group themselves around the old mode in the course of but a few generations. In evolutionary speculation the different processes which have been included under the general term of horticultural improvement have not been carefully enough distinguished, and this looseness of expression has led to error and confusion. To this we shall refer later.

As has already been suggested, the fourth type of variation is that in which the changes are not gradual and flowing, but sudden and unmediated. Saltatory variations they have sometimes been called, but it seems better to speak of the individual transitions as steps and of variation by steps. To this class belong those known as bud variations, in which certain buds of an individual give rise to a branch of essentially different character from the rest of the plant. Another group includes the so-called single variations of Darwin. These are solitary individuals of characteristics markedly different from those of their parents or neighbors, which are at rare intervals to be found in a garden bed and which sometimes become the ancestors of a new and constant race. Many examples of such might be given, but these may be reserved for later paragraphs. Each type has advantages and disadvantages as material for study. The bud variations demonstrate beyond question the genetic connection with another form and show most perfectly their unmediated origin.

They must always be investigated with caution, since they are likely to be produced from hybrids or from plants belonging to varieties with mixed and only partially fixed characters. The single variations have the disadvantage of leaving some uncertainty as to the possible origin of the plant. The new form appears suddenly and unmediatedly. Nothing is known of it until it is there, and then it is usually too late to be absolutely sure of the source or purity of the seed and many other considerations of importance.

The impression that these steps are longer than the range of common or fluctuating variations, and perhaps differ from this type of variation chiefly in their magnitude, is very common, and not a surprising one. One sometimes hears the remark that the mutation theory merely disregards the smaller and considers only the larger variations.

But the difference is not merely quantitative, it is qualitative as well. The difference between these steps is often smaller than the range of common variability. The numerous minor species into which *Draba verna* has been divided differ from each other very slightly, and less than the range of the fluctuating variability of some species, or even less than the different parts of a single individual of some others, and yet years of cultivation have shown them to be sharply differentiated and constant systematic units. Other examples might be given to establish this point, but the space will be better employed in giving a very apt illustration used by Galton, showing the differences between mutation and variation. A polyhedron rolling upon a smooth surface has a centre of gravity for every side. On any side it may oscillate back and forth without passing away from the center of gravity of the side upon which it rests. This may represent common or fluctuating variability. But a greater force may change the centre of gravity of the polyhedron, and then it will come to rest upon another side where it may oscillate indefinitely in response to some small force until some force as great as that which caused the original change, again changes the centre and moves it backward or forward. A change in the centre of gravity and the consequent shifting of the whole polyhedron represents a step or mutation. The number of the sides of the poly-

hedron determines the magnitude of the steps; increase this number, and the difference in character between the successive positions becomes less and less. And to carry the figures a little farther and let the path of the rolling polyhedron represent the history of the species, we see that each change of position has represented a step —a mutation.

THE COMPARATIVE DATA OF THE MUTATION THEORY.

The supporters of the theory of natural selection must show not only that common variability may be carried to the extent of specific differences by the requirements of natural forces, and the modification thus secured then become fixed, so as to be independent of these forces in heredity, but it must also account for discontinuity—the absence of transitional stages of the nature of those attributable to fluctuating variability. The mutation theory, if it is to be considered on a basis of equality with the old theory, must show that while explaining their discontinuity, the assumption of a variability by steps, a special species-forming variability, can account for the high degree of differentiation exhibited in the vegetable kingdom.

One of the most essential things is to examine as searchingly as possible the nature of the species, to have clearly in mind just what is to be understood by the term "species" as used in the terminology of experimental and comparative evolution. Once it was assumed that the Linnæan species were created, just as earlier it had been thought that genera had that distinction. Since this is no longer held to be true, the conception of the species has been linked with the binary nomenclature—that which was given a generic and a specific name was a species. Earlier in this essay some emphasis was laid upon the statement that species are collective groups. Linnæus himself recognized this fact, and it was pointed out by others of the old masters of systematic botany. Collective species are imperative necessities in all fields of biological work. The grouping of plants into species has the same value as their arrangement in genera and higher systematic divisions but must be regarded as equally artificial.

Let us take an illustration. A systematist may examine material which falls clearly into three or four distinct species, composed each of a number of minor forms, separated by wide differences over which no fluctuating variability can furnish transitions. Later collections or those from widely distant localities may fill the gaps, and the problem becomes an exceedingly difficult one. The whole series is composed of a large number of slightly differing units, each well characterized, but in the opinion of the student of that particular group of too small denomination to merit separate specific designation. So long as certain groups of the slightly differing forms were lacking the others stood well isolated and could be given specific rank, but when the series becomes complete there appears no point at which it can be divided. This group might represent a wider range of variation than all the other species of the genus combined, but, so long as all the differences are of lesser rank than those selected as specific, consistency demands that it be retained a simple species or that the whole genus be resolved into its most elementary forms.

Had some of the elementary types been exterminated or never collected, the several species originally described would have stood as valid, valid from the standpoint of the descriptive systematist, but not from that of the experimental evolutionist who must recognize as the unit only the smallest constant type, the so-called elements of the species, if such exist,—and to show this is the primary object of the mutation theory—and not artificial conveniences.

The demand has always been made that the origin of a species be the subject of direct observation, and, while the broad theory of evolution is so firmly established on comparative and historical grounds that the observation of the origin of a species is no longer needed to convince the learned world of the validity of the theory, the requirement is a perfectly legitimate one.

The emphasis which has frequently been laid upon the slowness with which selection may modify and transform species has doubtless had its influence in deterring investigators from approaching the subject of the influence of selection from an experimental point

of view, but a more serious hindrance has been the vagueness of ideas concernig species, subspecies, and varieties.

It is obviously unreasonable to demand that the origin of a Linnæan or collective species be observed. The origin of such an artificial group is a historical phenomenon, consisting in the elimination by natural selection of certain of the elementary types in the chain and the consequent dividing of the one continuous series into smaller ones separated by gaps of greater or less extent. The origin of these species is a subject for historical and comparative but not for experimental investigations.

But when it is admitted that it is unfair to ask for the observed origin or still more for the experimental production of artificial groups of forms, there still remains another and very serious difficulty. So soon as evidence for the origin of a new type from another is brought forward, it is immediately opposed by the assertion that it is only a *variety* of the species from which it sprung. It is discouraging to the investigator to have the results of laborious researches set aside by a mere juggling of ill defined terms in that all forms whose origin is more or less definitely known are designated as varieties, and it becomes necessary to examine the nature of the most minute systematic units as carefully as the larger artificial groups.

Few things are more variable than the terms variability and variety. The comprehension of all forms—except hybrids—whose origin is more or less definitely known, under the term variety includes the improved or acclimatized races and the widely different single or sudden variations. In nature, on the other hand, varieties are regarded by the best systematists as those forms which are differentiated by a single characteristic. A very good example is that of the common and the purple Jamestown weed, described as two species by Linnæus but now made species and variety, since the only difference is the presence of coloring matter in the stem, leaves, and flower of the purple one. Such varieties are usually just as independent and just as constant in culture as the best species. Variety in this case then means only a special kind of species. "Varieties are only small species," says Darwin.

Varieties differ greatly from the numerous elementary species of Jordan. The latter differ in almost all their characters. If it is true that species in nature consist of a number of individual and constant types, then it is to be supposed that those selected by man for cultivation will also be composed of a number of types.

Pliny recognized numerous varieties of many cultivated plants, 43 of pears, 29 of apples, 10 of plums, 8 of cherries, etc., while the *Théatre d'agriculture,* published in 1600, listed a few more. It is quite possible that some of these forms originated in cultivation or even under the influence of cultivation, but whence they came is entirely unknown, and it is quite possible that all the different types were present when agriculture began and were brought as such under cultivation from the same or different habitats. There is no reason to assume that wild plants were brought into cultivation but a single time, and with repeated gatherings of the seed of wild plants from different localities the probability of securing a number of different types would be greatly increased.

In the beginning of the nineteenth century the wheat fields of Le Couteur on the Isle of Jersey were found to be not a homogeneous culture but exhibiting numerous well defined types of which Professor La Grasco recognized at least twenty-three. Seed from these was selected, and when grown separately they showed themselves pure and constant, and the better kinds were cultivated and profitably placed in the trade, where some are still to be found.

In Scotland much the same method was followed with various cereals by Patrick Shirreff and with closely corresponding results. Several types hitherto unrecognized were found, the seed increased for two or more generations, and placed at once on the market. These experiments show that wheat, oats, and barley were at that time a mixture of constant subspecies, just as has been seen for wild plants. Of the origin of these subspecies as little is known in one case as in the other.

Perhaps of even greater interest to the general reader than the origin of the different varieties of cultivated cereals is that of the history of the hundreds of varieties in our orchards and vineyards. The common origin of our varieties of apples and pears need not be

questioned, but except in the case of a few of the more recent introductions, for which there is a trustworthy record, this must be regarded as a deduction from the accepted fact of descent rather than historically recorded data. Some of the most interesting observations available are those of a Belgian plant breeder, Van Mons, of the first half of the nineteenth century, who introduced many of the best-known sorts of the present time. He disclaims the credit of the production of any new forms, "*La nature seule crée.*" All the forms he introduced he found growing wild, mostly in the Ardennes.

With cultivation in the garden the wild scrubs lose their thorns, and the coarse, small fruits become larger, fleshier, and juicier. But form, flavor. color, and other distinguishing characteristics do not originate in or through cultivation. They are already present, and the only effect of cultivation is to bring them to their fullest perfection. Van Mons was so fully cnvinced of the independence and constancy of his forms that he called them subspecies instead of varieties. To introduce a new sort, then, one must not select seeds of the best cultivated types but rather, according to Van Mons, seek for the seed of a small, poor fruit, but of a type as yet unknown.

Flax, red clover, and the poppy show such sup-species, or minor species. The principal types of *Chrysanthemum indicum* were brought as such into Europe, and more recent varieties have been derived from these by crossing. Numerous so-called varieties, even many monstrosities, are almost as old as the cultivation of the species itself and are figured or listed in the old herbals, while of the most important cultivated plants, such as hyacinths, tulips, and Ranunculus hundreds of varieties were known.

Only one more illustration may be given. The cactus dahlias of the present time are so universally known and admired that the history of their origin might be read with interest. A Holland grower received from a correspondent in Mexico a chest of bulbs, roots, rhizomes, and tubers, which had spoiled in transit so that only a single tuber produced a plant. This was the dahlia, and when in flower was found to be of the hitherto unknown cactus type. From it the numerous cactus varieties have been produced

by crossing with forms already cultivated. All effort to find the plant in the region where the chest was filled has been fruitless—all that is known is that it was there. How it originated is not known. New forms are wont to be found only in the largest cultures. Wier found his cut-leaved maple among about a million seedlings, and the first double dahlias were found in a culture of about 10,000 plants.

The agreement of wild and cultivated species in their polymorphic composition has been considered. The importance of the composite nature of cultivated forms has so impressed itself upon breeders and some of the earlier botanists as to lead to the saying: "The first essential for the production of something new is to possess it already." In these paragraphs the fact has been emphasized particularly that not nearly all the cultivated forms are to be considered as originating in or especially through cultivation. The establishment of this thesis is a strong argument against the theory of natural selection, for which the triumphs of cultural selection have been the strongest pillars of support. But it must not be inferred that new forms never do originate in cultivation. It is to a few trustworthy records of this occurrence that we shall now turn. The data available for this examination strongly emphasize the assumption of a fundamental difference between the improved races and subspecies. So convinced of this was Von Rümker, for instance, that he divided his well known work on the breeding of wheat into two sections, the one treating of selection for improvement, the other of production of new forms. The first of these has, according to him, the object of fixing, more sharply differentiating, and increasing the superiority of characters already present, while the second consists rather in the search for new forms which occasionally appear. One of the best known records is that of *Chelidonium laciniatum*. This form, characterized by its deeply cut leaves and petals, was first observed in a bed of *Chelidonium majus* in the garden of a Heidelberg apothecary in the year 1590. Neither he nor any other botanist to whom he sent specimens of his novelty had ever seen or found described a similar form, nor has it been found wild up to the present time. Since the time of its appearance it has been and is still

constant with no reversion to the characteristics of the typical *C. majus*.

In a garden Cyclamen, in which the impossibility of crossing prevents the assumption of hybrid origin, a number of forms seem to have originated in this same way. A strawberry without runners, the Gaillou strawberry was found as a single example among a lot of the ordinary type and has been found to be quite constant. Cauliflower and kohlrabi of the kitchen garden, and other varieties as well, originated as monstrosities of the common cabbage, and the same might be shown of other well-fixed garden forms.

Sometimes these new types have originated independently in widely separated localities or at different times. Several good examples might be given of the discovery of similar and constant novelties in different regions. A double Syringa was recently found in a garden and was introduced as an entirely new form, and was so considered until it was found recorded in an old work bearing the date of 1671.

Other examples of constant and heritable subspecies and varieties might be given, but enough have been mentioned to illustrate the comparative data of the mutation theory. This has led to the conclusion that the gradual development of the elementary species has not yet been demonstrated among cultivated plants, but that numerous cases of the sudden origin of new "species" may be considered valid or at least highly probable. Considering the fewness of the cases in which the new forms are isolated and kept from the swamping incident to free cross-fertilization, they show themselves very generally heritable and as constant as the older so-called good species.

THE EXPERIMENTAL DATA OF THE MUTATION THEORY.

a. THE INSUFFICIENCY OF VARIABILITY WITH SELECTION.

It is of great interest to establish on comparative grounds the theory that the discontinuity of systematic units as they exist at the present time is due to discontinuity of variation. But, however strong this comparative evidence may be, however complete the series of forms showing no transition stages, it cannot carry with

it the conviction which experimental proof may offer, and it is the production of this experimental proof which lends such weight to the mutation theory.

In the preceding pages variation has been divided into four classes, systematic polymorphism, the polymorphism of hybrids, common or fluctuating varibility, and mutation. Systematic polymorphism is largely a problem of descriptive botany and concerns only indirectly the experimental evolutionist. The different combinations of elementary characteristics found in hybrids offers a most promising field for experimental work, and to it the second volume of *Die Mutationstheorie* is a contribution. Our present purpose is to examine carefully the nature of the third and fourth classes of variability, fluctuating or flowing variability, and mutation. and fourth classes of variability, fluctuating or flowing variability, and mutation.

Comparative evidence may stand for much, but it is upon experimental grounds that the greatest weight must be laid. The evidence in favor of the selection theory is drawn in great part from the data of artificial selection. This has necessarily constituted the mass of the experimental data of the selection theory. Beyond this it has depended upon comparative investigations, and this evidence has been very satisfactory for the establishment of the theory of morphological and historical descent.

Experimental work may be undertaken along three different lines. The ability of selection to develop new and constant forms may be investigated as searchingly as possible, the hypothesis of a special species-forming variability may be given the greatest weight by actual observation of the origin of distinct and constant forms, and finally the conduct of the elementary characters of plants may be studied in hybrids. All of these methods have been employed in the development of the mutation theory, but it is with only the first two that we are concerned in the present paper.

In approaching the question as to the ability of natural selection to develop new species it is first necessary to examine the validity of the data upon which much of the theoretical discussion has been based. It may be safely asserted that in the past too much

theoretical significance has been attached to the practical achievements of horticulturists. By many every new garden form has been attributed to artificial selection. To this we shall recur later.

It must be borne in mind that practical plant breeding is carried on not for the purpose of collecting scientific data, but for financial profit, and while the breeder may be quite willing or anxious to gain an insight into the scientific laws underlying his profession, it is usually more profitable to experiment at haphazard and upon a larger scale, saving the promising individuals and burning the rest, than to undertake the detailed and laborious researches necessary to the formation of detailed laws of conduct. For this reason accurate accounts of experiments are usually dispensed with. When a particularly desirable form is secured, the process by which it was obtained is generally unknown. It came from a series of broad and varied experiments, but which particular condition or combination was the fortunate one is unknown or alleged only from a chance memory, which may or may not be trusted. An accurate and painstaking record of all experiments would usually cost more than it is worth to the man of practical aims. The biologist must necessarily work with the fewest and simplest factors possible to avoid the hopeless confusion incident to an admission of all factors. The originator of new forms, on the other hand, seeeks to increase rather than to decrease the multiplicity of factors in his experiment. Systematic polymorphism, crossing, enrichment of the soil, mutation and the gradual improvement by selection may all be thrown together indiscriminately in the hope that something good may be secured. That many thousands of failures are made, matters little so long as there is occasionally something good which pays for the whole experiment.

To attribute the whole success of horticultural improvements to selection is far from the truth. There are several quite distinct processes to be borne in mind. There is the improvement by hybridization with newly discovered and in some respects more desirable forms. Genera which are very rich in species or those in which there have been occasional discoveries of new types in little known

regions have been crossed in so many different ways that they present an insoluble tangle of garden forms which owe their origin almost exclusively to varied combination of the elements of the various wild forms. Examples of this are Fuchsia, Dahlia, Chrysanthemum, Begonia, Gladiolus, Caladium, and Amaryllus. Hybridization is a so much surer and easier method of securing forms that it is rarely to the interest of the breeder to exclude the possibility of crossing. Only when a new race is to be fixed or where the process of pure selection has been decided upon is this done. And only when this factor is excluded have the results of the breeder any significance for the selection theory. In selecting examples to illustrate the effect of horticultural selection, too great care cannot be exercised in making sure that there is no possibility of a previous cross-fertilization by the wind or insects.

Horticultural and agricultural "improvement" may be here compared. The varieties introduced every year in greater or less numbers by trade gardeners may be new elementary species or varieties, originating suddenly and unexpectedly in the garden, they may be newly introduced elementary species or varieties hitherto uncultivated, or they may be hybrids representing new combinations. These forms are then freed from the effect of previous crossing, a process which requires a period of time of from two to five years, which time is also necessary for obtaining sufficient seed to make it profitable to offer the variety to the trade. The entire profit of such a new form is in the first year of its introduction, since, once introduced, seed may be supplied by any firm or by the kitchen garden as well as by the one first offering the novelty. For this reason a newly originated or discovered from is often offered to the public simultaneously by a combination of several houses so that the first year's profits may be the greater.

With the true improved races the case is quite different. These depend upon the careful and constant selection of the best individuals, and the one who secures the best forms may be sure of his yearly profits from the sale of seeds until some rival introduces a more desirable article, since constant selection is required to maintain the betterment secured and seed cannot be saved from the

crops grown for commercial purposes, but must frequently be secured anew from the original source or from some other where selection is just as keen as in the original.

To account for the origin of species by natural selection it must be assumed that this selection may carry the differences offered by common variability to the extent of specific characteristics, and that the degree of differentiation from the original type shall then become independent of the selective influences. The first of these assumptions is quite possible, since common variability in some forms shows a wider range than that offered by the specific limits of others; but that selection may so fix these that they become independent of it, can be admitted only with a much greater weight of evidence than that at present available.

Before speaking at greater length of this let us examine a few cases in point. To secure the horticultural betterment which has so often served as proof for the theory of natural selection does not require the great length of time many suppose, nor is the improvement unlimited in extent. The universally known fact that certain plants have been in cultivation for centuries and are widely different from the wild forms from which we assume they have sprung does not necessarily indicate that these forms have been constantly and uniformly improved by selection during this period, or indeed that they owe their fixed characteristics to selection at all. In our orchards we have a vast number of varieties of apples, but the apple is in its wild state a very polymorphic genus. This and hybridization, and the origin of new forms by mutation in culture, are to be taken into consideration.

Historical evidence is almost, if not quite, wanting. Almost the only method of obtaining an insight into the action of selection is the study of such records of exact experimentation as are available, and the accumulation of such other data as opportunity will permit. That available is very limited in amount.

In making this examination of the sufficiency of natural selection it seems that two points are of especial importance. The one is the rapidity with which an individual characteristic may be brought to the maximum of its possible improvement, and the

other is the certainty of regression when the selective influence is removed. The most of the betterment of a form may be secured in from two to five generations, depending largely upon the number of characteristics to be modified. Lévêque improved the wild carrot so much in from three to five generations that the roots were as fleshy and suitable for culinary purposes as the common cultivated form. Carrière had the same success with the wild radish, and Buckmann found that the wild parsnip could be rapidly improved by cultivation. An unusually interesting case is furnished by certain alpine primulas which have developed two seasonal forms, one of which blossoms before and the other after the cutting of the principal harvest of hay. Of course, in this case it cannot be determined whether it is a case of slow selective or of sudden and unmediated chance adaptation to the peculiar conditions. One of the finest series of data for the study of selection is furnished by the history of the sugar beet, the lines of improvement being not too complex, and the record of a nature suitable for statistical comparison.

Of the origin of the sugar beet we can say little. At the beginning of the nineteenth century numerous varieties were known, but of their origin we know as little as of most cultivated plants. It is simply with the selective improvement of the beet that we wish to deal. From 1830 to 1840 Vilmorin selected the sugar beet with reference to external characteristics, but not until 1851 did he test the sugar content of the individual roots, when he found that they contained an amount of sugar varying from 7 to 14 per cent. The seeds of those richest in sugar were selected for the next planting, and in the second generation he secured beets with 21 per cent. of sugar. The methods available were not highly accurate or convenient, permitting an examination of but a limited number of specimens, but it is probable that he found too little rather than too much sugar. In 1874, when the vastly improved method of the determination of the sugar content by means of the polariscope and selection according to its indications was begun, the sugar content was 10-14 per cent., in poor years showing a mean of 10 per cent., in good years 12-14 per cent., while variations from 9.5 to 17.5 per

cent. were not rare. The new method spread gradually in Germany from 1878 to 1881. At present an immense number of beets are polarized each year in a large manufactory. The sugar percentages are found to form a very symmetrical curve which is in close agreement with Quetelet's law. Some individual figures from the establishment of a Holland firm may be of interest. In 1892 roots containing less than 14 per cent. were not utilized for seed, those with 14 to 16 per cent. furnished plants the seed of which was sold, while those with 16 to 18 per cent. furnished seed plants for their own race, the so-called élite, from whose seed the beets to be polarized in the next generation were to be grown. In this year only four out of 180,000 specimens examined showed more than 18 per cent. of sugar. Since 1892 the number of roots polarized has been increased to 300,000 with the result that the upper limit of 21 per cent. of sugar was reached. The plants commercially grown from the seed offered to the trade showed a mean of 13 to 14 per cent. of sugar.

The commercial profit to be derived from increasing the percentage of sugar from 7-8 to 14-16 or over is evidently enormous, but when it is noted that the highest limit reached in the hundreds of thousands of specimens tested by the Holland firm coincides with the highest percentage observed by Vilmorin, 21 per cent., it will be seen that twenty-five generations of selection seem to have produced very little biological difference. Other races grown under different conditions may yield an upper limit of 26 per cent., but it must be borne in mind that the present scope of the beet sugar industry offers the possibility of higher maxima.

Selection is not carried on with regard to the sugar content alone but for all other characters which have been found of importance, only about one tenth of the harvest being selected in the field for the final chemical examination. The development of the sugar content of the beet has been slow and more or less uniform, but this is attributable in a large measure to the gradual improvement of methods. Never has the betterment become independent of selection. With the exceedingly sharp selection described above the quantity of seed procurable is far too small for commercial purposes, and an intermediate generation must be grown to increase

this quantity. Even in this one generation the reversion is very great, and should more than two generations be grown it would be so great that the gain of the laborious selection for the so-called élite culture would be lost. A half a century of labor and experience has produced results of the highest commercial importance, but so far as can be seen, has accomplished nothing toward the establishment of a constant systematic form.

Here we may not take the space necessary for a discussion of the cereals in their relation to the problem before us. It must suffice to say that the evidence they offer confirms that furnished by the sugar beet—that selection does not lead to the formation of constant characters but only to a betterment which is dependent upon constant selection for its maintenance.

We may not discuss further comparative data. In our necessarily much condensed review this seems the most suitable place to mention one of the most interesting chapters in the first volume of Professor DeVries's work—a chapter in which he has, as everywhere else in his researches, sought to introduce the experimental methods. The simplification of the study of variation by the recognition of the two fundamentally different types of variability is not sufficient. Each of these must be subjected to the most searching experimental study.

One method is the placing in opposition of the two apparently different influences. Selection and nutrition forms one of the most suggestive chapters of evolutionary literature. The detailed treatment of this interesting section is quite out of question in the present place, since the description of the experiments and explanation of the statistical methods used in the exact comparisons would lead too far. We must simply state in the most general way that the common or fluctuating variability of certain plants was accurately measured by the statistical methods which have shown such a development of recent years, and then the influence of selection and mutation upon the variability measured as they acted separately and combined or antagonistically. The effect of the best possible conditions of nutrition in its broadest sense, and of the sharpest selection were compared and then opposed to

each other by giving the plants the best possible conditions for growth while selection was made of the poorest individuals for seed plants or vice versa. Experiments were made with the fruit lengths of *Oenothera Lamarckiana,* the number of branches in the inflorescence of the Umbelliferæ and the number of rays of the composite flowers. The results of these studies show that when selection and nutrition are opposed to each other sometimes the one and sometimes the other has the controlling influence, while again it remains undecided. The investigations indicate that selection and nutrition influence the plant in the same way, and that it is a matter of circumstance which predominates in its influence. In other words, to express this more significantly, fluctuating variability is a manifestation of the physiology of nutrition. The external causes of mutation are as yet quite unknown.

Of such vital importance to the mutation theory is the establishment of the hypothesis that selection does not lead to the origin of specific characters, that we shall give here, in the form of a summary, the supporting evidence for this hypothesis, after which we must pass directly to the second class of evidence for the mutation theory, the direct observation of the origin of species or specific characters.

1. Statistical investigations have replaced the old vague idea of an all-sided variability with that of linear variation in a plus or minus direction. Existing characters may be increased in magnitude, but something new does not come into existence, and since the differentiation of organisms depends in the main upon the development of new characteristics, the necessary material is not to be found in linear variations.

2. The view that linear variation is unlimited and may be carried farther by the selection of centuries than by that of a few years is entirely unsupported. In the betterment of individual characteristics, two or three generations under favorable conditions, and three to five generations under ordinary conditions, are sufficient to bring the improvement to its maximum. Further selection in the absence of special conditions serves only to maintain what has already been secured.

3. The limits of selection are no more sharply marked than those of fluctuating variability. By vastly increasing the number of individuals the range of variability may be slightly increased, and the same is true of selection. This has been illustrated in the development of the sugar beet. The idea that with selection variability in a certain direction increases is quite contrary to the better known cases in which progress soon becomes less rapid and gradually ceases. Darwin's idea that in the first years of their introduction into cultivation plants showed themselves increasingly more variable, probably depended in part upon the discovery of elementary species, latent or overlooked until that time.

4. Upon every selection there follows a regression the greater the sharper the selection, and independent of its duration. Apparently more than one half of the betterment is lost in each generation. In improvement a doubling, or, when selection is in the opposite direction, a halving of the value of the original characteristic is all that may generally be obtained in the best cases, and usually much less is attainable; the striking examples furnished by fleshy roots and fruits furnishing only an apparent exception.

5. The principal difference between improved races and species—and even the most minute elementary species—is the inconstancy of the former and the constancy of the latter. The improved races are just as dependent upon selection for their permanence as for their development; when selection ceases to act, the race characteristics revert to the original type in about the same time as that required for their development.

6. Constant improvement of the methods of selection may secure constant betterment of the race. Every improvement of method signifies a sharper selection, but if the method remain the same the limit attainable is constant.

7. Scientific investigation should, so far as possible, be confined to individual characteristics. The laws of correlation will rarely allow this. In practical work, since general betterment is desired the time necessary is greater, just twice the number of generations being required with two characteristics with cultures of the same extent.

8. Every improved race is adapted to a special environment, soil, climate, and manuring. Only when their special requirements are met is the promised yield assured. In this they agree with the local races of the wild flora.

9. The importance of natural selection as influencing artificial selection in the fields has often been taken too little into account in theoretical biology. Cold, frost, moisture, crowding, lateness in maturing "select" in the field with the same surety as the best breeder. In rare cases, as in acclimatization where the object is mainly elimination of those not adapted to the conditions, natural and artificial selection coöperate, but in most cases they strongly oppose each other, natural selection tending to favor the stronger, but according to the special taste of the breeder, less desirable individuals. The problem of the breeder becomes then first the maintenance of his race.

The discussion here given to the first of the three paths open to the experimental evolutionist in considering the problem of the origin of species is meager and with many gaps, but it must suffice for the present while we pass by the second to indicate some of the results which have been obtained in the third, the path which Professor DeVries has broken for the scientific world and the one in which it is to be hoped that other investigators will eagerly follow.

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[TO BE CONCLUDED.]